



**University of
Zurich**^{UZH}

**Zurich Open Repository and
Archive**

University of Zurich
University Library
Strickhofstrasse 39
CH-8057 Zurich
www.zora.uzh.ch

Year: 2015

Family living: an overlooked but pivotal social system to understand the evolution of cooperative breeding

Drobniak, S M ; Wagner, G ; Mourocq, E ; Griesser, M

Abstract: Cooperative breeding occurs in several major animal phyla, predominantly in arthropods and chordates. A number of comparative analyses have focused on understanding the evolution of cooperative breeding, yielding mixed, inconclusive, and often phyla-specific findings. We argue that much of this ambiguity results from an erroneous classification of social systems into noncooperatively and cooperatively breeding species. The shortcomings of this assumption are apparent among birds where noncooperative species constitute a heterogeneous group: some species are clearly non-family living, with offspring dispersing at or shortly after nutritional independency, whereas other species form persistent family groups through offspring delaying their dispersal substantially beyond independency. Here, we propose an objective, life history-based criterion classifying noncooperative bird species into non-family living and family living species. We demonstrate that by using the family time (the time offspring remain with its parent/s beyond independence) and body size-scaled reproductive investment, we are able to differentiate 2 groups with contrasting life histories. Our classification matches seasonal environmental variation experienced by different species: family living species postpone dispersal beyond the onset of less favorable autumn conditions. We discuss the consequences of this new social system classification for evolutionary and ecological research, potentially allowing solutions to some of the most intriguing riddles in the evolutionary history of birds—and cooperative behavior itself.

DOI: <https://doi.org/10.1093/beheco/arv015>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-122199>

Journal Article

Accepted Version

Originally published at:

Drobniak, S M; Wagner, G; Mourocq, E; Griesser, M (2015). Family living: an overlooked but pivotal social system to understand the evolution of cooperative breeding. *Behavioral Ecology*, 26(3):805-811.

DOI: <https://doi.org/10.1093/beheco/arv015>

**Family living: an overlooked but pivotal social system to understand the
evolution of cooperative breeding**

Running title: Family breeding – an overlooked social system

Szymon M. Drobnia^{1*}, Gretchen Wagner¹, Emeline Mourocq¹, Michael Griesser¹

¹ Anthropological Institute and Museum, University of Zurich, Switzerland

* Corresponding author: Szymon Drobnia, Anthropological Institute and Museum,
University of Zurich, Winterthurerstrasse 190, CH 8057 Zurich, Switzerland; tel. +41 (0)44
635 54 34; e-mail: szymonmarian.drobnia@uzh.ch

Abstract

Cooperative breeding occurs in several major animal phyla, predominantly in arthropods and chordates. A number of comparative analyses have focused on understanding the evolution of cooperative breeding, yielding mixed, inconclusive and often phyla-specific findings. We argue that much of this ambiguity results from an erroneous classification of social systems into non-cooperatively and cooperatively breeding species. The shortcomings of this assumption are apparent among birds where non-cooperative species constitute a heterogeneous group: some species are clearly non-family living, with offspring dispersing at or shortly after nutritional independency, whereas other species form persistent family-groups through offspring delaying their dispersal substantially beyond independency. Here, we propose an objective, life-history based criterion classifying non-cooperative bird species into non-family and family living species. We demonstrate that by using the family time (the time offspring remain with its parent/s beyond independence) and body size-scaled reproductive investment, we are able to differentiate two groups with contrasting life-histories. Our classification matches seasonal environmental variation experienced by different species: family living species postpone dispersal beyond the onset of less favourable autumn conditions. We discuss the consequences of this new social-system classification for evolutionary and ecological research, potentially allowing solutions to some of the most intriguing riddles in the evolutionary history of birds – and cooperative behaviour itself.

Lay summary

Bird social systems are more diverse than previously appreciated – here we show that defining an intermediate social system, family living, where individuals postpone their dispersal but do not cooperate in reproduction, is a natural extension of the widely accepted two-categories system (non-cooperative versus cooperative breeding). The evolution of prolonged association between offspring and parents appears to be possible in cases where it extends into the unfavourable period of environmental conditions, i.e. into autumn/winter season.

Keywords: family breeding, cooperation, comparative study, life-history, dispersal, parental care, social system

Introduction

Understanding cooperation is fundamental to evolutionary biology, and this question was already seen by Darwin as a great challenge to his theory of natural selection (Darwin, 1859). Hamilton's theory of kin selection (Hamilton, 1964) resolved the apparent altruism of cooperation among related individuals, and provided us with a framework to study the evolution of cooperation in kin groups, and particularly its most interesting case – cooperative breeding. In many birds and mammals that breed cooperatively, young from previous broods remain with their parents beyond independence and help to raise younger siblings (Hatchwell, 2009), although non-kin individuals can also engage in cooperative breeding (Riehl, 2013).

Given the abundance of cooperative breeding in birds and mammals, and diversity of life-histories and ecological covariates observed in both of these groups, they have served as model groups for studying the evolution of reproductive cooperation. In both groups, large scale comparative analyses of cooperative breeding have been published recently, taking advantage of complete and accurate phylogenetic data available for birds and mammals (Feeney et al., 2013; Jetz and Rubenstein, 2011; Lukas and Clutton-Brock, 2012). In all of these studies, as well as preceding work (Arnold and Owens, 1998; Cockburn, 1998, 2003), social systems were described in a binary fashion: species were either classified as cooperative breeders, where individuals help raising offspring that are not their own, or as non-cooperative, where only parents are involved in raising offspring. The presence of helpers is a straightforward criterion, easily observable in the field, and provides an unequivocal definition of cooperative breeding, and could be further revised to account for kin-based and non-kin cooperation (Riehl, 2013). However, this binary categorisation fails to account for an important feature of animal social systems – namely the formation of kin groups in the absence of cooperative breeding.

Kin groups usually arise when offspring delay their dispersal beyond independency and remain with their parents and siblings for a given period of time (Russell, 2000). In some cases this period (termed ‘family time’ henceforth) is short, often short enough that such a strategy can be undistinguishable from dispersing right after reaching independence. However in other cases persistent family groups are formed, which usually is associated with various forms of non-reproductive kin cooperation (Covas and Griesser, 2007; Dickinson and McGowan, 2005; Griesser et al., 2006). A number of studies have pointed out that family living is an essential first step for the formation of cooperative breeding, as in almost all cooperatively breeding species offspring have first to delay dispersal and remain with their parents before they can become a helper at their parents nest (Ekman et al., 2001; Ekman et al., 2004; Emlen, 1994). Thus, family living is likely to represent an intermediate strategy, fitting somewhere in the continuum of social systems between pair breeders and cooperative breeders. As such one might expect fundamental life-history differences between family living, non-family living and cooperative breeding species, and consequently merging non-family living and family living species might be partly responsible for equivocal and inconsistent results of comparative studies obtained so far (Covas and Griesser, 2007; Griesser and Barnaby, 2010). Yet, how should family living species be distinguished objectively from non-family living species?

Family time could provide a biological benchmark for this distinction. However, it would be too simplistic to classify as non-family living species only those where offspring disperse from parents, or parents abandon their offspring after reaching nutritional independence, as in many seabirds. Family times exhibit great variation and span from direct dispersal at independence to several years (Russell, 2000). Species with short family time most likely are ecologically and evolutionarily more similar to species with zero family time. Thus, a threshold value of family time is needed in order to classify family living species. In

such a way a continuous measure directly describing the degree of parent-offspring association could be transformed into a categorical descriptor, supplementing the existing “cooperative breeding” category. The difficulty is finding an objective classification of this continuous quantity (i.e. family time) allowing to extract such threshold.

Here, we address the problem of defining family living by using a large dataset of family time of nearly 750 bird species. We expect that evolution of delayed dispersal and family living would be associated with major changes in life-history traits, and thus we predict that the footprint of these evolutionary processes should be visible in differences between family living and non-family living species. This evolutionary history would be reflected in a number of key eco-evolutionary traits associated with reproduction. Such traits could be used as benchmarks of life-history changes that arose due to breeding either in pairs or in larger family groups. However, such benchmark trait can only be used to measure differences *between* two groups. Locating the positions of the splitting point separating the groups requires a focal continuous variable that should be a straightforward extension of the desired nominal classification. An obvious choice in our case is the family time – as the trait directly measuring the degree of post-independence parent-offspring association. A more difficult task is finding a suitable benchmark variable, the values of which could guide us on the scale of focal variable.

To this end we have used the body-size-scaled initial reproductive investment (Sibly et al., 2012) as the benchmark variable of choice. In a simple numerical framework use it to define an objective threshold value of family time that best separates family and non-family living species. Breeding investment is closely related to individual fitness and integrates various ecological and physiological factors that together shape the life-history of a species (Martin, 1987; Martin et al., 2006; Sibly et al., 2012). It is regarded as an accurate proxy of species reproductive strategy, placing it on the important slow-fast life-history axis.

Moreover, it is available for substantially more taxa than other life-history parameters and as such represents the most widespread fitness-related measure currently available. We not only demonstrate how family-time can be tied up with reproductive investment to yield the desired classification of family/non-family living species. We also discuss how our novel classification relates to the expected differences between non-family and family living species in terms of their life-history and ecology.

Methods and materials

The key temporal variable used in our study was family time, defined as the period of time the offspring delayed dispersal and stayed with their parents after reaching nutritional independence. We used unpublished data from a review paper (Russell, 2000) and the major handbooks of birds (Cramp et al., 1994; Del Hoyo et al., 2011; Higgins et al., 2007; Maclean and Robert, 1985; Poole, 2005) to collect data on the family time, together with detailed information on the remaining temporal characteristics of bird breeding (incubation period, nestling time, time to independence after leaving nest). The data on the reproductive investment (annual sum of clutch sizes per breeding pair in each species scaled by the female body mass, see below) were retrieved from a recent publication (Sibly et al., 2012), while we also gathered additional values on reproductive investment from the literature (see above). In total, we had data on family time, reproductive investment and egg mass for 712 species, covering all major clades defined by the low-level phylogenetic backbone derived by Hackett et al. (2008; see also Jetz et al. 2012 for more details). Deliberately we have removed cooperatively breeding species from all analyses – their status and classification do not require any additional clarification: a binary criterion exists (i.e. presence or absence of predominant reproductive cooperation) that unambiguously defines them as cooperating or otherwise.

We used a body weight-scaled key parameter of reproductive investment (productivity index; (Sibly et al., 2012)) calculated as:

$$\pi_m = \log (m_e \cdot n_e \cdot n_c / m_f),$$

where m_e – egg mass; n_e – number of eggs per clutch; n_c – number of clutches per year; m_f – average female body weight. We adapted the productivity index proposed by Sibly et al. (2012) and used female body mass instead of male-female averaged mass, as the body weight of females – i.e. the sex that physically produces the eggs – appears more appropriate as a reference for measuring reproductive investment. We repeatedly generated groups of family and non-family living species based on the family time threshold varying between 2 and 150 days. Thus, we explicitly assumed that birds with family time < 2 days are classified as non-family living, and species with family time > 150 days are classified as family living. We decided to stop at a family time of 150 days and classify all species with longer family times as family living for a number of reasons: (i) we do consider species with family time >150 days as being certainly above the threshold and thus surely family living species; (ii) beyond the 150 days threshold the sample size in the two groups becomes very unbalanced as we successively classify more species as non-family living and less as family living (Figure S1, for family time > 150 days there are less than 25 species in family living group and more than 650 species in the non-family living group) – which is likely to make the conclusion much less robust. For each of the 149 iterations a mean productivity index (π_m) value was calculated for non-family and family living species. We then looked for the family-time threshold value that generates the maximum absolute difference in mean π_m between the two social systems.

To explore further how our categorization of social systems coincided with ecological conditions that might influence its evolution, we investigated the distribution of inferred social systems in relation to yearly seasonal changes and the mean growing season of the species distribution. The mean growing season describes overall plant vegetation timing in a

given location (Michaletz et al., 2014) and strongly correlates with actual geographic location expressed as the absolute latitude of the centroid of species geographic distribution (Figure S6). All models were analyzed using a generalized linear mixed model with a binomial distribution (a two-states response variable: family living vs. non-family living; logit link function) in *MCMCglmm* (Hadfield 2010). The model included the phylogenetic effect to account for non-independence of species due to shared phylogenetic history. All runs were performed with 1000000 iterations, 250000 burn-in period, and samples taken from the posterior distribution of estimated fixed and random effect parameters every 1000 iterations (resulting in effective sample size of approx.1000). Phylogenetic signal was calculated as the intra-class correlation coefficient at the level of the phylogenetic random effect according to Hadfield (2014).

In order to ensure that the results are valid and do not result from statistical artifacts we have performed a number of validations based on simulation and bootstrapping. The details on each of the validation methods can be found in the Supplementary materials.

It is difficult to construct analytically sampling error measures for the estimated parameter. First – randomizing/resampling the data tends to generate functional relationships of several kinds between the difference in π_m and family time threshold (depending on the iteration we were able to fit e.g. logistic, polynomial, exponential to the resulting pattern). Thus, automatically extracting the threshold value – which could be used to construct approximate sampling distribution – is difficult. To provide a surrogate of sampling distribution we have used the following strategy: (i) we generated 1000 subsets of data by bootstrapping (resampling with replacement) rows of original dataset; (ii) for each subset performed threshold search; (iii) fitted a segmented piece-wise regression to the resulting pattern (package *segmented*; Muggeo, 2003) to extract the breaking point of the pattern, indicating the maximum observed value (most patterns either plateau or reach maximum at

this value; in both cases the breaking point accurately identifies the threshold – in case of the original pattern (Figure 1) this breaking point is equivalent to edge of the plateau, i.e. family time = 50 days); (iv) constructed a sampling distribution of 1000 estimated breaking points, which will necessarily be centered around the original estimated threshold.

Results

The shifting-threshold approach indicated a maximal difference in initial breeding investment between resulting non-family and family living species for a cut-off value of 50 days (Figure 1). Using this 50 days threshold resulted in 529 species classified as non-family living and 104 species being classified as family living. The remaining 79 species are cooperative breeders and were not included in our analyses as the definition of cooperative breeding is unambiguous. Bootstrapping of family-time values reveals noise around the original pattern, mostly generated by resampling random species from a continuum of family times – vast majority of samples however successfully replicate the 50 days threshold (see histogram, Figure 1).

Four different validation methods all supported the 50 days threshold (see Supplementary Materials and methods). In particular, phylogenetically corrected values recapitulated the pattern observed in raw means (Figure S1). Randomized samples (see Supplementary Materials and methods: validation 2 and 3) did not exhibit the pattern observed in the original data (Figures S2 and S3). Moreover, the pattern also was confirmed when equal sizes of social systems groups were used by resampling them for each threshold value with replacement (see Supplementary Materials and methods: validation 4, Figure S5). It is important to note that the choice of the start of the plateau in Figure 1 is only one

possibility. One might argue that instead of using the first observed plateau observation it might be more suitable to shift the threshold further along the plateau toward greater values of family time, or place it at some other unambiguous points along the estimated line (e.g. the inflection point located between 10 and 50 days of family time, equivalent to roughly a half of maximum observed difference between family and non-family breeding species). However, any other placement of the threshold would result in a less parsimonious conclusion (putting the threshold further on the plateau would result in including as non-family breeding individuals those that do not contribute to predicted differences in reproductive allocation and at the same time have abnormally long family times) or in classification that is not stable in terms of life-history parameters (putting the cut-off at the inflection point would yield where differences between the two resulting groups would be very sensitive to even small changes of the chosen classification threshold).

Independently of family-time considerations, an interesting effect concerning total breeding period became apparent in our data. Combined data on incubation and nestling time with the time to independence and family time indicated that in most non-family living species offspring dispersed the latest 150 days after the onset of breeding (Figure 2). In contrast, in the majority of family living species dispersal of offspring occurred later than 150 days after the onset of breeding (Figure 2). In non-family living species offspring dispersal occurred later than 150 in only 14 cases days and the majority of those species have the centroid of their geographical distribution in low latitude regions (Figure 3). Similarly, the majority of family living species where offspring disperse before 150 days from the start of breeding ($n = 24$ species) occurred mostly in temperate regions or resided in both temperate and tropical climate (Figure 3). This was further confirmed by an interaction between total breeding period (total time from egg laying to offspring dispersal) and the mean growing season of the species distribution in a mixed model looking at the probability of observing a

particular breeding system (Table S1). The interaction indicates that the probability of being a family living species increases with total time spent with parents (sum of all pre-dispersal periods) in regions of long mean growing season (i.e. low latitudes), but decreases with increasing total time spent with parents in regions where the mean growing season is shorter (i.e. latitude increases) (Table S1). The generalized mixed model confirmed that the social system (family living vs. non-family breeding) is highly phylogenetically structured (phylogenetic heritability and its 95% highest posterior density interval: on the link function scale 0.67 (0.54; 0.87); on the scale of data: 0.94 (0.87; 1.06)).

The estimated threshold that we use to categorise social systems in birds coincides with a natural hiatus in the distribution of family times (Figure 4). Excluding family times equal to zero, the distribution is bimodal with a ridge around the value of 50 days (Figure 4). Interestingly, when including zero family times, the distribution is trimodal as most species tend to disperse directly after achieving independence. This first gap separates species having zero and non-zero family time and thus, for reasons explained in the Introduction and the Materials & Methods, cannot be used as a suitable threshold to define families.

Discussion

Our results confirm that social breeding systems are more heterogeneous than previously appreciated (but see Russell, 2000). Using birds as a model system and a central life-history trait, the annual reproductive investment, we demonstrate that non-cooperatively breeding species are heterogeneous in terms of the post-independence offspring dispersal and can be further divided into two distinct categories. One of the most easily observable features of social breeding – namely, the formation of persistent groups composed of kin individuals delaying their dispersal – occurs also in species lacking any traces of reproductive

cooperation. However, contrary to reproductive cooperation, classifying family living species is more ambiguous as it cannot be assessed based on a bi-categorical descriptive behaviour. The fact that offspring in some species remain some time beyond independency with their parents may just reflect variation in dispersal timing as found in many species, or behavioural inertia in moving from one phase of life cycle to the other, particularly if short delays in dispersal are costly neither to parents nor offspring. Our approach provides an objective way of finding the critical family-time value that results in the biggest difference between the two social systems. Moreover, the result coincides with naturally observed discontinuity in the distribution of family-times in our larger set (i.e. including species for which we did not have the productivity index and that could not be included in the main analysis). While similar considerations relating delayed dispersal and breeding ecology have been made in evolutionary biology (e.g. Russell et al. 2004), our approach is unique in providing an actual definition that is based on measurable properties of bird reproductive biology. Importantly, our analyses have proven to be robust to all statistical artefacts that might generate similar results – all validation procedures confirmed the presence of the observed pattern and supported its uniqueness (in both randomization analyses that break association between productivity and family time the pattern disappeared).

Annual productivity (π_m) is a central and fundamental life-history variable (Sibly et al., 2012), reflecting adaptations of bird life-histories to varying ecological conditions (Griebeler et al., 2010; Lack, 1968; Sibly et al., 2012). Thus, it is also affecting the link between social systems and reproductive strategies (Arnold and Owens, 1998; Cockburn, 1998; Covas and Griesser, 2007; Emlen, 1994). Splitting non-family living and family living species according to a threshold value of family time equal to 50 days maximizes the difference in annual investment observed in these two groups. On average, non-family living species have a higher annual productivity compared to family living ones, confirming studies indicating that

298 delayed dispersal is more frequent in species with low adult mortalities and low reproductive
299 output (Arnold and Owens, 1998; Ekman et al., 2001; Russell et al., 2004). The difference is
300 substantial – non-family living species produce on average 1.5-times more eggs per year per
301 unit of body mass than family living taxa. It is possible that the strategy of forming family
302 groups buffers-out costs of rearing offspring and results in being able to maintain similar
303 overall success with a lower annual productivity. Alternatively, delayed dispersal, while being
304 beneficial to the offspring, may be costly for parents – forcing them to decrease their
305 reproductive output considerably and favouring offspring quality over quantity. Although our
306 study does not point to one particular alternative, we hope it will stimulate further research
307 towards understanding costs and benefits of family living.

308 Why is the 50 days threshold a biologically meaningful cut-off to define family living?
309 In non-tropical climatic zones the period of year comprising the most favourable conditions
310 for breeding spans over approx. 150 days (rounded to full months; mean 155.72 ± 10.49 days
311 (www.weatherbase.com, accessed 05/12/2014); favourable conditions defined as months with
312 average temperature greater or equal to 11°C, the temperature associated with an average
313 large-scale vegetation onset in temperate locations and the start of the optimal photosynthetic
314 activity (Morison and Morecroft, 2006)) and starts roughly in April/May in the northern
315 hemisphere (respectively in September/October in the southern hemisphere), concluding with
316 a decrease in food abundance and an onset of less favourable conditions in September in the
317 northern hemisphere (respectively March in the southern hemisphere) (Morison and
318 Morecroft, 2006). For most non-family living species the total breeding period is shorter than
319 150 days (Figure 2) and hence does not progress beyond this boundary of worsening
320 conditions. The total breeding period of most family living birds, however, exceeds 150 days
321 (Figure 2, 3). The outcome of our analysis reveals an ecological footprint of the evolution of
322 family living with respect to seasonally occurring unfavourable conditions (Russell, 2000).

Delaying dispersal beyond autumn may only be possible in species where offspring can benefit from prolonged association with their parents, increasing their survival (Covas and Griesser, 2007; Ekman et al., 2001). Our approach indicates that these benefits may outweigh costs of family living only if it is associated with long-enough association of individuals forming a family group.

Relating family and non-family living to the assumed 150 days period of unfavourable conditions (Figure 3) reveals yet another interesting bio-geographical pattern: all pair-breeding species that live in high latitudes lie below this line, whereas all the remaining (pair and family breeding) species laying above this line live exclusively in mid- and low-latitudes. Thus, prolonged parental care and delaying dispersal seem to be ecologically constrained in high latitudes but provide clear advantage in lower latitudes, shifting the distribution of kin-group forming species toward lower latitudes (Russell, 2000). The nature of this constraint requires further research: it is possible that solely climatic constraints prevents birds from delaying dispersal into harsher and less viable conditions – however other factors contributing to delayed dispersal (e.g. access to high quality territories inherited from parents) also may be latitude-constrained.

Interestingly, in both groups there are species that do not match this 150-days criterion. Apart from random noise in the data (i.e. inaccurate data on family time – or timing of any other part of the reproductive cycle), such cases may be explained by accounting for geographical distribution of such species. Most non-family living species crossing the 150 days' timeline come from low absolute latitude regions (i.e. tropical/sub-tropical) or are widespread species with mixed climatic preferences. Similarly, family living species with total breeding period below 150 days tend to be temperate-climate ones. Thus, mismatches occur mostly in cases where the 150-days threshold may not be accurate and limiting, supporting our result.

The consequences of this new classification for our understanding of the evolution of social behaviour in birds still remain to be explored. Our preliminary results not presented here indicate that discrepancies between the traditional and new classification of social breeding systems are substantial. For example, our classification significantly alters observed associations between social system and environmental unpredictability in terms of environmental dependency of cooperative breeding, extending and greatly clarifying earlier analyses (e.g. Jetz and Rubenstein, 2011). Our analyses indicate that merging together non-family and family breeders erroneously associates two very different strategies, and in terms of environmental sensitivity family breeders are more similar to cooperative breeders (Griesser et al., 2014, Abstracts of the 1st Modern Phylogenetic Comparative Methods conference). Moreover, family living taxa exhibit markedly higher levels of sexual body size dimorphism compared to non-family living and cooperatively breeding species, which emphasizes the great evolutionary uniqueness of family breeding in terms of sexual selection pressure and how it is related to overall life-history patterns in birds (Drobniak et al., 2014, Abstracts of the 15th International Behavioral Ecology Congress).

To conclude, our life-history based approach shows that cooperative-breeding and non-family living are not the only alternatives on the scale of social modes in birds. Family living in the absence of cooperative breeding represents an intermediate state, which hitherto has not received sufficient attention. More importantly, family living may represent a transition stage in the evolution of cooperative breeding as almost all cooperative breeding birds live in family groups (Riehl, 2013). Using family living as an intermediate social system one can provide a more parsimonious, multistage description of how cooperative breeding might have evolved in birds (Covas and Griesser, 2007; Ekman et al., 2004; Emlen, 1994). Appreciating this social system will open new research perspectives and solve existing inconsistencies in our understanding of the evolution of cooperation.

Acknowledgments

We thank Shinichi Nakagawa and two anonymous reviewers for their valuable insights and comments that helped to improve this manuscript. The research was funded by the Swiss National Science Foundation, grant number PP00P3_150752 and PP00P3_123520 (to MG).

References

- Arnold KE, Owens IPF, 1998. Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proc R Soc B* 265:739-745.
- Cockburn A, 1998. Evolution of helping behavior in cooperatively breeding birds. *Annu Rev Ecol Syst* 29:141-177.
- Cockburn A, 2003. Cooperative breeding in oscine passerines: does sociality inhibit speciation? *Proc R Soc B* 270:2207-2214.
- Covas R, Griesser M, 2007. Life history and the evolution of family living in birds. *Proc R Soc B* 274:1349-1357.
- Cramp S, Simmons KE, Perrins CM, Brooks DJ, 1994. Handbook of the birds of Europe, the Middle East and North Africa. Oxford: Oxford University Press.
- Darwin C, 1859. On the origin of species. London: John Murray.
- Del Hoyo J, Elliot A, Sargatal J, Christie DA, 2011. Handbook of the Birds of the World. Barcelona: Lynx Editions.
- Dickinson JL, McGowan A, 2005. Winter resource wealth drive's delayed dispersal and family-group living in western bluebirds. *Proceedings of the Royal Society B-Biological Sciences* 272:2423-2428.
- Ekman J, Baglione V, Eggers S, Griesser M, 2001. Delayed dispersal: Living under the reign of nepotistic parents. *Auk* 118:1-10.
- Ekman J, Dickinson JL, Hatchwell BJ, Griesser M, 2004. Delayed dispersal. In: Koenig WD, Dickinson JL, editors. *Ecology and Evolution of Cooperative Breeding in Birds* Cambridge: Cambridge University Press.
- Emlen ST, 1994. Benefits, Constraints And The Evolution Of The Family. *Trends Ecol Evol* 9:282-285.
- Feeney WE, Medina I, Somveille M, Heinsohn R, Hall M, Mulder R, Stein J, Kilner R, Langmore NE, 2013. Brood Parasitism and the Evolution of Cooperative Breeding in Birds. *Science* 342:1506-1508.
- Griebeler EM, Caprano T, Bohning-Gaese K, 2010. Evolution of avian clutch size along latitudinal gradients: do seasonality, nest predation or breeding season length matter? *J Evolution Biol* 23:888-901. doi: DOI 10.1111/j.1420-9101.2010.01958.x.
- Griesser M, Barnaby J, 2010. The role of nepotism and competition for the evolution of avian families. New York: Nova Publisher.
- Griesser M, Nystrand M, Ekman J, 2006. Reduced mortality selects for family cohesion in a social species. *Proc R Soc B* 273:1881-1886.
- Hamilton WD, 1964. Genetical Evolution of Social Behaviour I. *Journal of Theoretical Biology* 7:1-&.
- Hatchwell BJ, 2009. The evolution of cooperative breeding in birds: kinship, dispersal and life history. *Philosophical Transactions of the Royal Society B-Biological Sciences* 364:3217-3227. doi: 10.1098/rstb.2009.0109.

- Higgins PJ, Marchant S, Peter JM, Cowling S, Davies J, 2007. Handbook of Australian, New Zealand & Antarctic Birds: Oxford University Press.
- Jetz W, Rubenstein DR, 2011. Environmental Uncertainty and the Global Biogeography of Cooperative Breeding in Birds. *Current Biology* 21:72-78. doi: 10.1016/j.cub.2010.11.075.
- Lack D, 1968. Ecological adaptations for breeding in birds. London: Methuen.
- Lukas D, Clutton-Brock T, 2012. Life histories and the evolution of cooperative breeding in mammals. *Proceedings of the Royal Society B: Biological Sciences* 279:4065-4070. doi: 10.1098/rspb.2012.1433.
- Maclean GL, Robert A, 1985. Roberts' birds of southern Africa: Trustees of the John Voelcker Bird Book Fund Cape Town.
- Martin TE, 1987. Food as a limit on breeding birds - a life-history perspective. *Annual Review of Ecology and Systematics* 18:453-487.
- Martin TE, Bassar RD, Bassar SK, Fontaine JJ, Lloyd P, Mathewson HA, Niklison AM, Chalfoun A, 2006. Life-history and ecological correlates of geographic variation in egg and clutch mass among passerine species. *Evolution* 60:390-398.
- Michaletz ST, Cheng D, Kerkhoff AJ, Enquist BJ, 2014. Convergence of terrestrial plant production across global climate gradients. *Nature* 512:39-43. doi: 10.1038/nature13470.
- Morison JIL, Morecroft MD, 2006. Plant growth and climate change. Oxford ; Ames, Iowa: Blackwell Pub.
- Muggeo VMR, 2003. Estimating regression models with unknown break-points. *Stat Med* 22:3055-3071. doi: Doi 10.1002/Sim.1545.
- Poole A, 2005. The birds of North America online. Cornell Laboratory of Ornithology, Ithaca, NY Available via <http://bnabirds.cornelledu/BNA>.
- Riehl C, 2013. Evolutionary routes to non-kin cooperative breeding in birds. *Proceedings of the Royal Society B: Biological Sciences* 280:20132245.
- Russell EM, 2000. Avian life histories: Is extended parental care the southern secret? *Emu* 100:377-399. doi: Doi 10.1071/Mu0005s.
- Russell EM, Yom-Tov Y, Geffen E, 2004. Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. *Behavioral Ecology* 15:831-838.
- Sibly RM, Witt CC, Wright NA, Venditti C, Jetz W, Brown JH, 2012. Energetics, lifestyle, and reproduction in birds. *P Natl Acad Sci USA* 109:10937-10941. doi: DOI 10.1073/pnas.1206512109.

Figure 1. Difference in annual mass-scaled productivity index (π_m) between family living and non-family living species in relation to the family-time threshold used to differentiate the two groups. Blue line represent original pattern, grey lines depict patterns obtained for bootstrapping samples drawn from the data. The approximate sampling distribution of the threshold value of family-time is shown as a histogram on the horizontal axis.

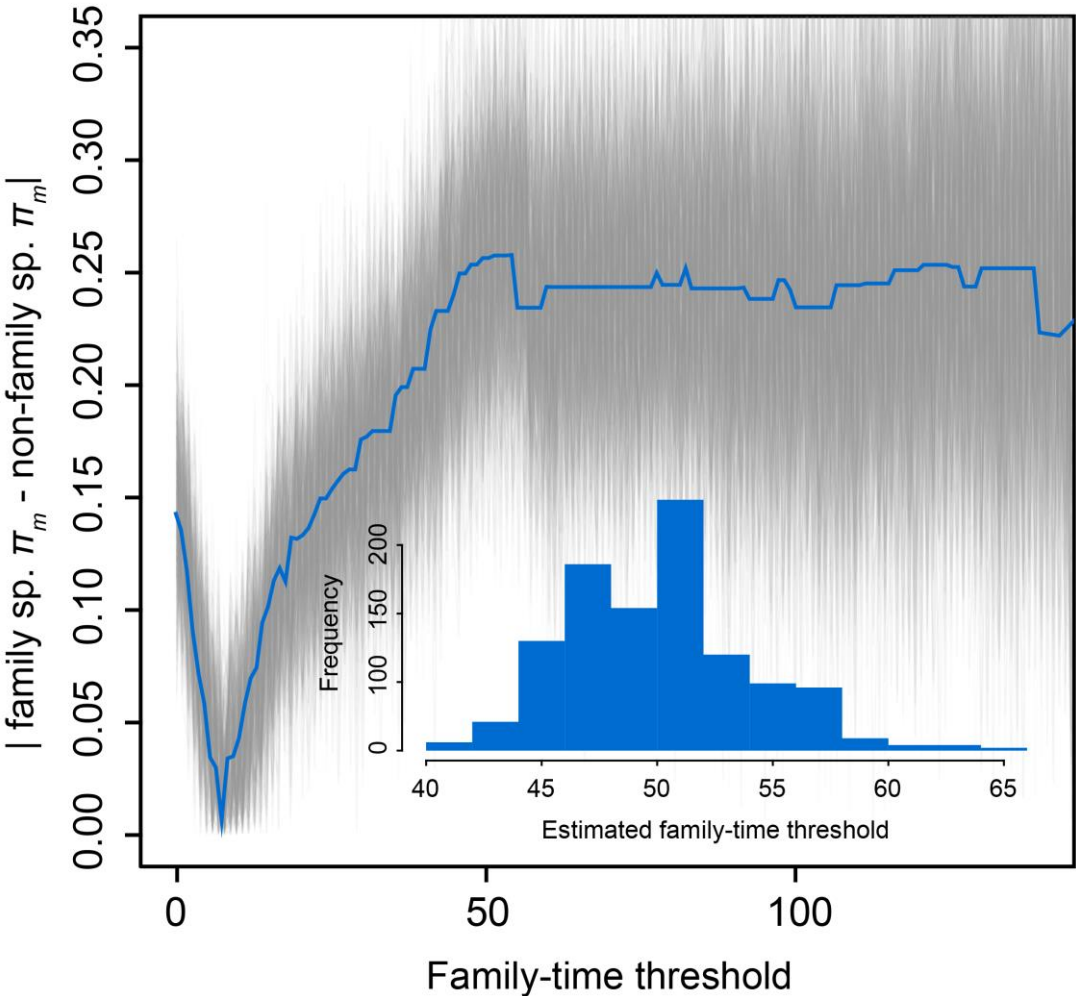


Figure 2. The distribution of total times that offspring spend with their parents, subdivided into respective periods of the lifecycle and in relation to three categories of social breeding defined using our approach. The 150 days limit is indicated with a dashed line (see the Discussion section for more details).

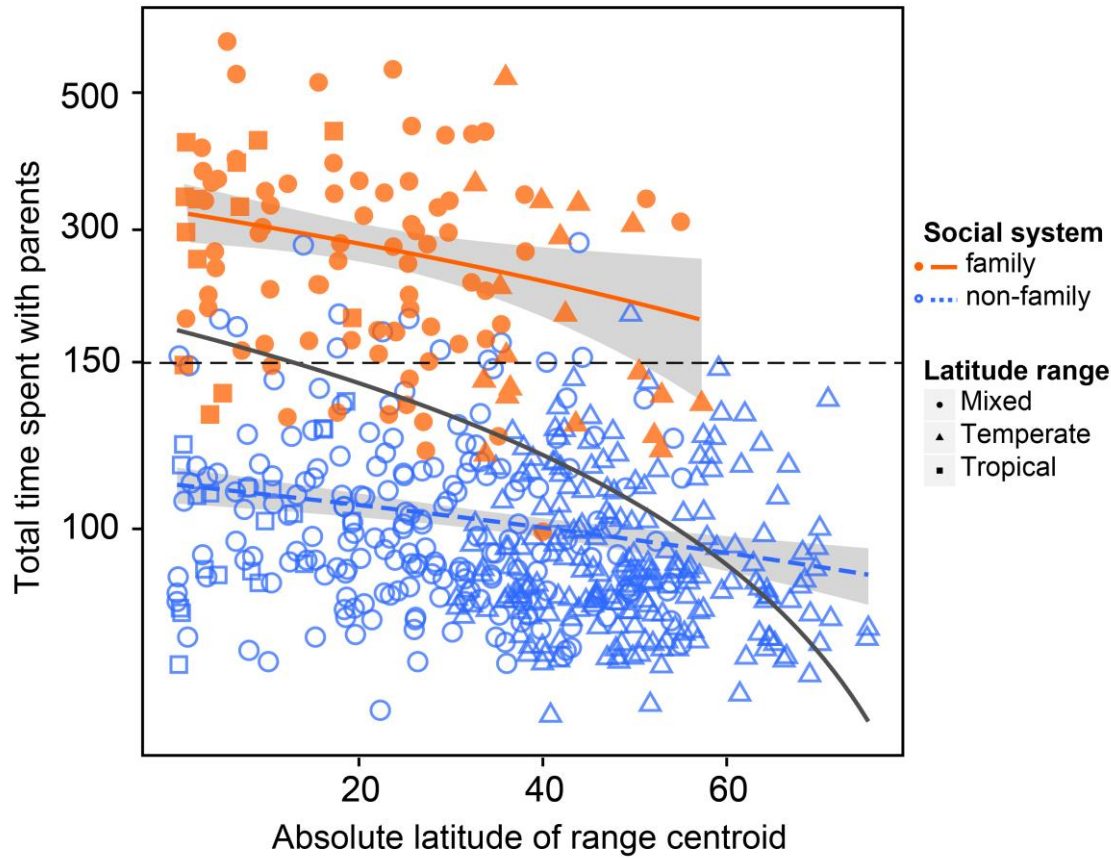


Figure 3. Association between the total time offspring spent with their parents (from onset of incubation to dispersal, in days), the mean growing season of species distribution and the range of latitudes occupied by each species. Black line depicts overall relationship in all species, coloured lines show relationships in the two social breeding systems. The 150 days cut-off (see text) is indicated with a dashed line.

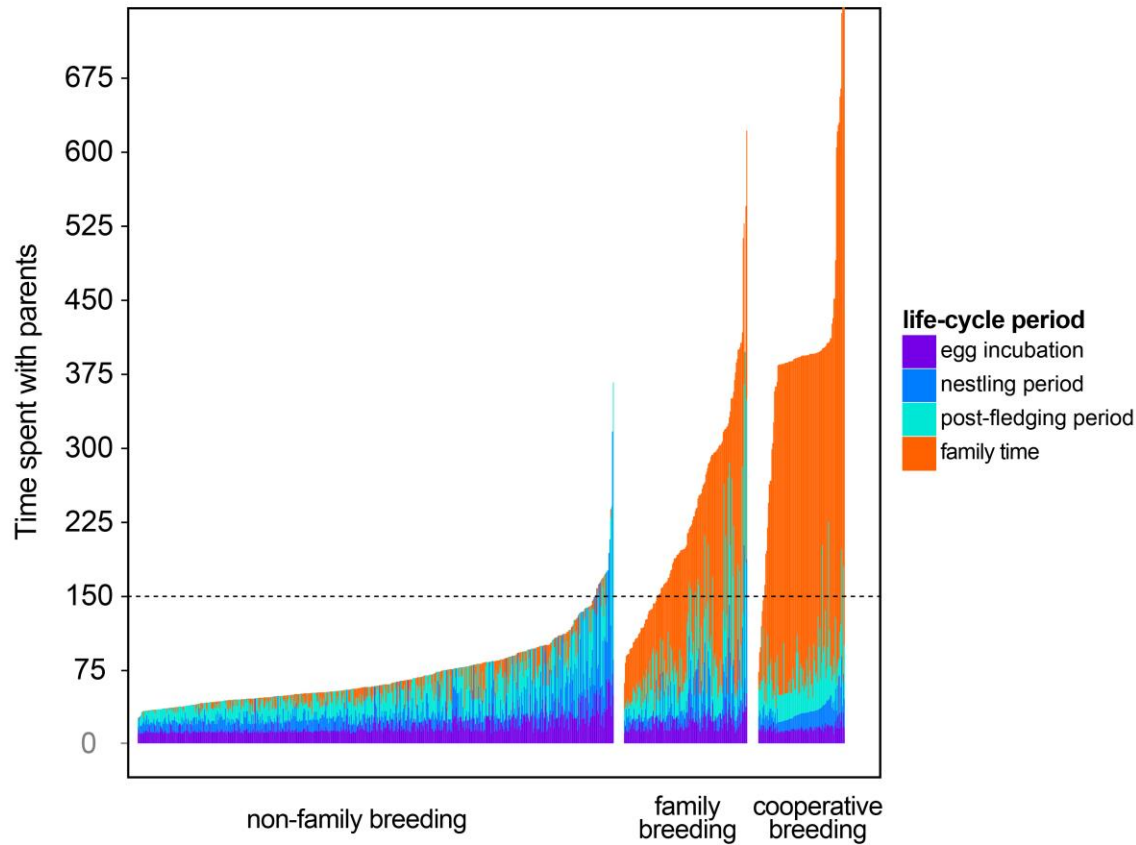
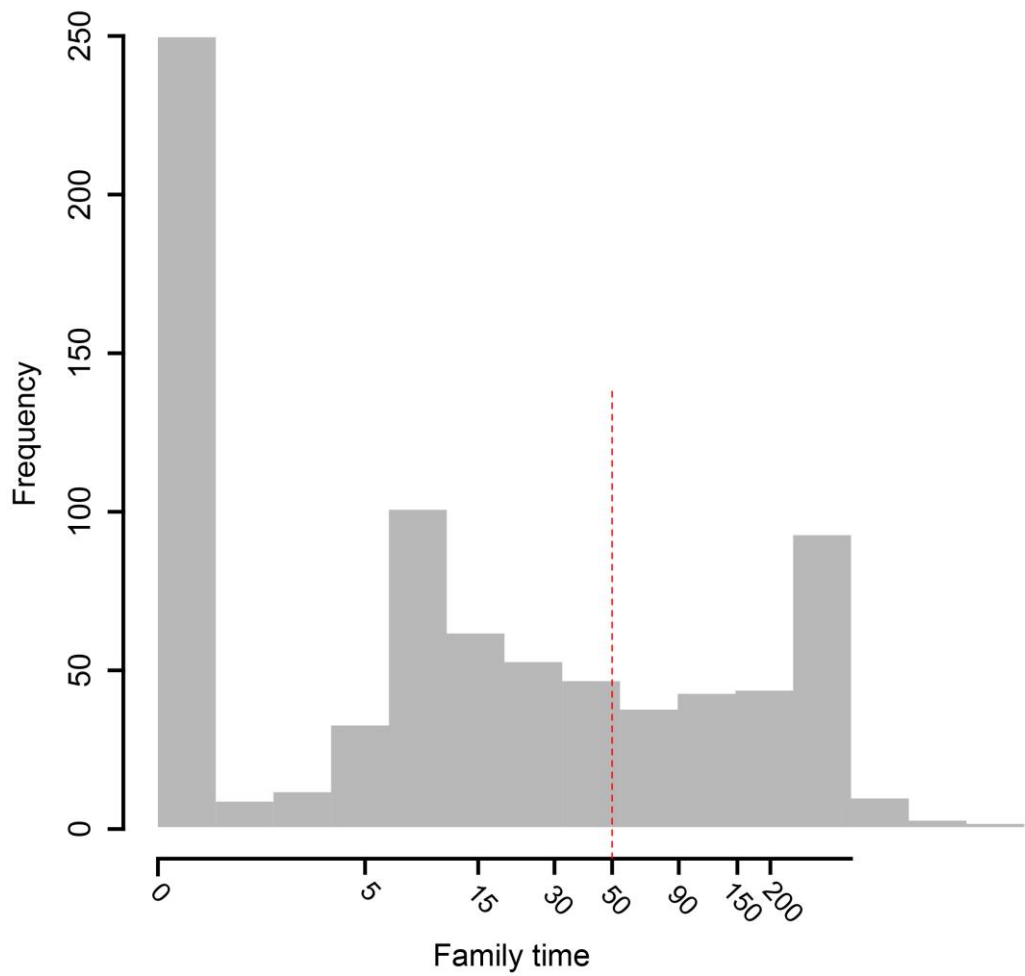


Figure 4. Distribution of family times in 1103 bird species. Red dashed line indicates the 50 days family time threshold that was chosen to separate family living and non-family living species.



Supplementary Materials and methods

We used four different ways of validating the results and ensuring its biological integrity:

- 1) **Phylogenetic signal:** to exclude the possibility that the observed patterns are generated only by a strong interdependence of closely related taxa, we generated for each family time threshold a phylogenetically corrected difference between family- and non-family living species. To do so, we fitted at each family time threshold a phylogenetic linear mixed model with π_m as a response variable and social status as a predictor. The differences between family living and non-family living birds were calculated by specifying a contrast that compared these two groups in the linear model (Figure S1).
- 2) **Statistical artifact not related to biology of studied species:** to verify that our result is visible only in the original configuration of π_m and family times we have randomized our data by reshuffling the family time column 1000 times (and thus effectively breaking any family time – productivity index associations). For each of 1000 randomizations we repeated the original procedure of searching for a threshold family time value described above (Figure S2).
- 3) **Statistical artifact related to linear trend:** family time is weakly correlated with Sibly index. Thus, to ensure that the pattern did not result from the presence of this relationship we generated 1000 samples from a linear model defined by the slope, intercept and residual variance observed in the original data. For each of 1000 randomizations we repeated the original procedure of searching for a threshold family time value (Figure S3).
- 4) **Difference in sample sizes:** shifting the family time threshold changes continuously the size of the two groups (family vs. non-family living) (Figure S4). To ensure that the differences did not arise simply because of the imbalance of group sizes, we repeated the original threshold search procedure, but for each iteration's family time cut-off we calculated mean π_m for family and non-family living species using 200 observations resampled with replacement from respective social systems groups. This way we ensured that for each family-time cut-off the calculation of mean π_m was based on equal sample size of 200 observations (Figure S5).

Table S1. Results from the generalized linear mixed model looking at the relationship between social system, total breeding period (see text) and geographical location.

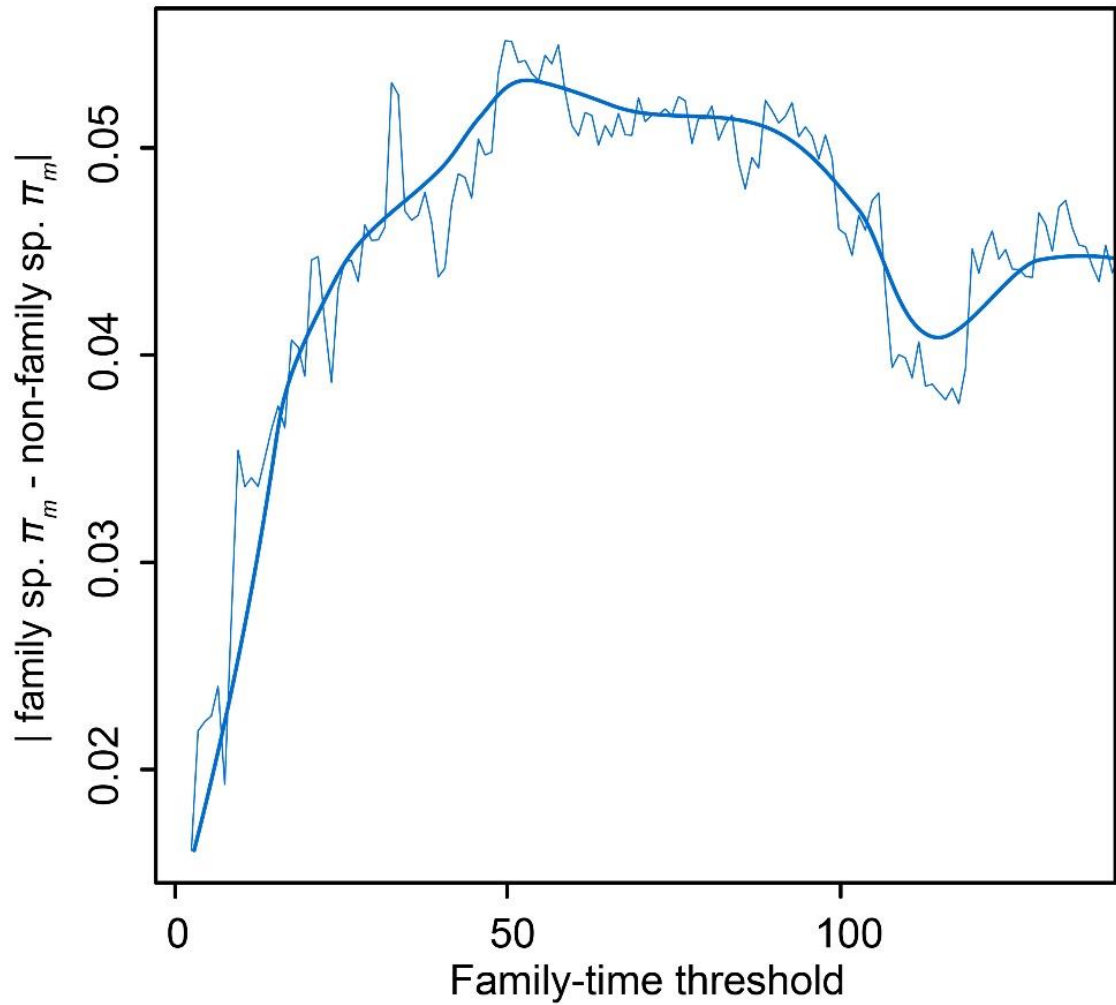
Fixed effects

Model term	Estimate	Lower 95% CI	Upper 95% CI	P _{MCMC}
Intercept	-1.654	-5.370	2.380	0.438
Total breeding period	-0.335	-5.932	-3.367	<0.001
Mean growing season duration (MGS)	-4.549	-1.544	0.860	0.594
Total breeding period × MGS	1.020	0.756	1.301	<0.001

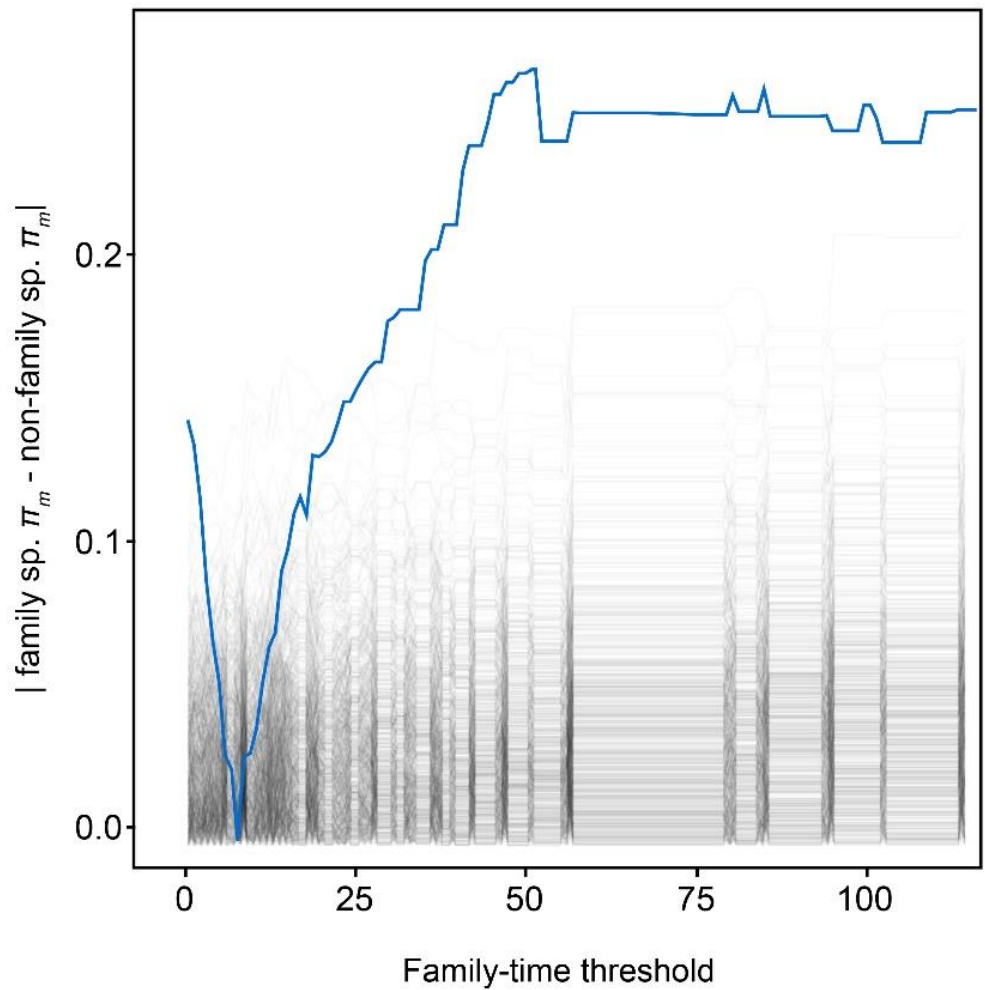
Random effects (residual variance fixed at V=1 by convention)

Random effect	Estimate	Lower 95% CI	Upper 95% CI
Phylogenetic effect	11.660	3.959	21.810

Figure S1. Replication of the original analysis but with phylogenetic correction. The plot depicts relationship between the difference in productivity index between non-family and family breeding species in relation to the threshold value of family time. Thin line – original pattern, thick line – LOESS smoother fitted to the pattern to better show the overall shape. (see point 1 in validation section of Materials and methods).



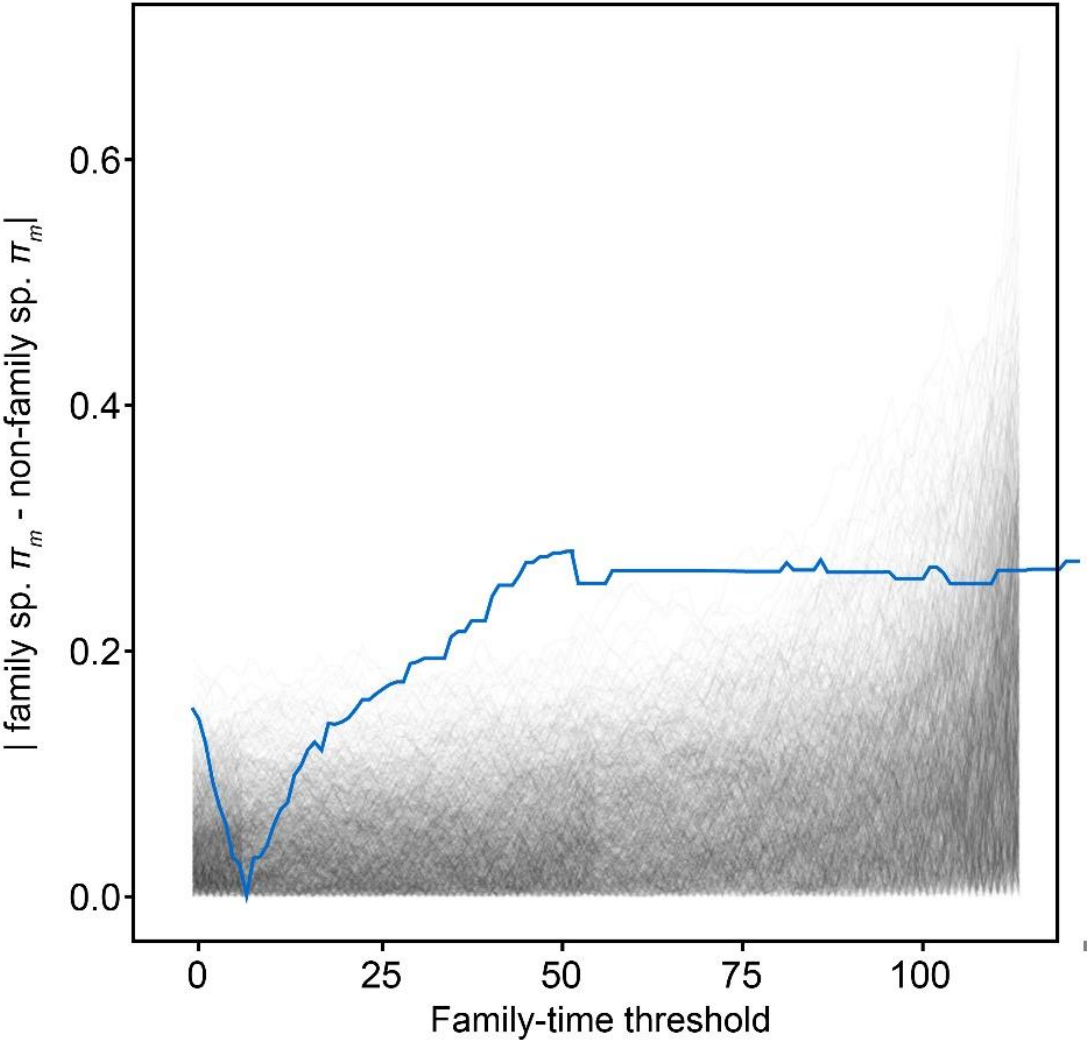
538 Figure S2. Original pattern (blue) and 1000 analogous curves obtained from randomized data. (see
539 point 2 in validation section of Materials and methods)



540

541

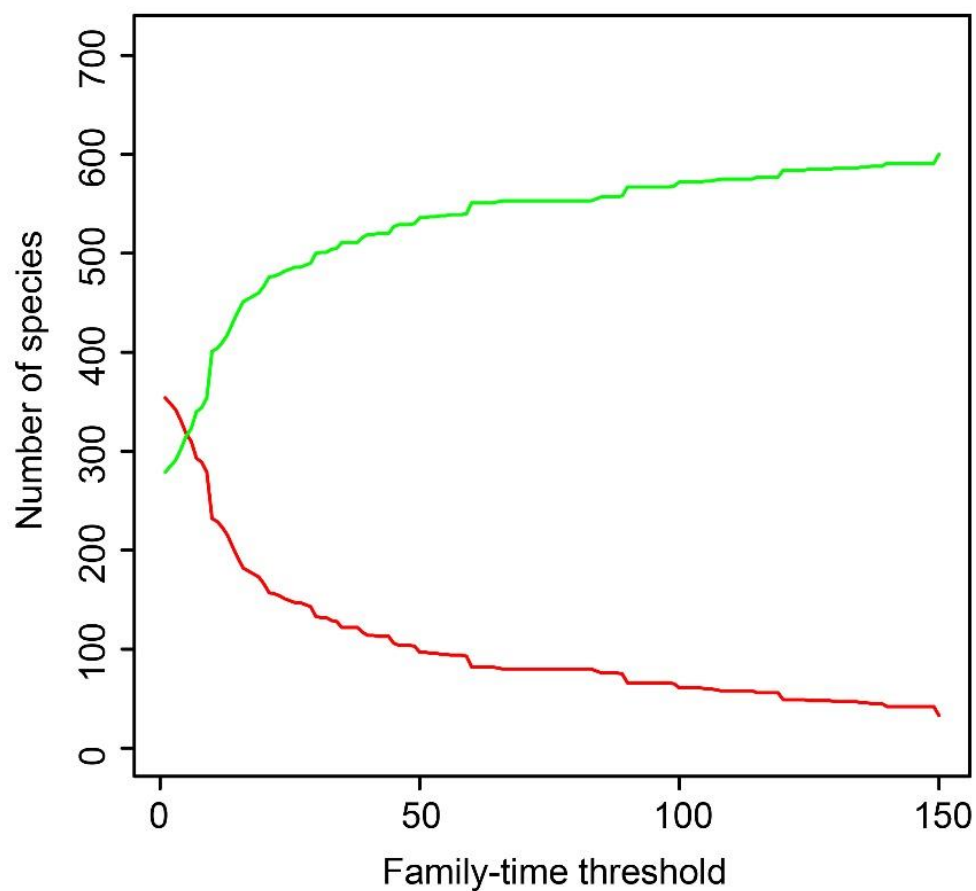
542 Figure S3. Original pattern and 1000analogous curves obtained from randomized data. Here the data
543 was not only randomized but also ensured to follow the same linear trend as in original data. (see point
544 3 in validation section of Materials and methods)



545

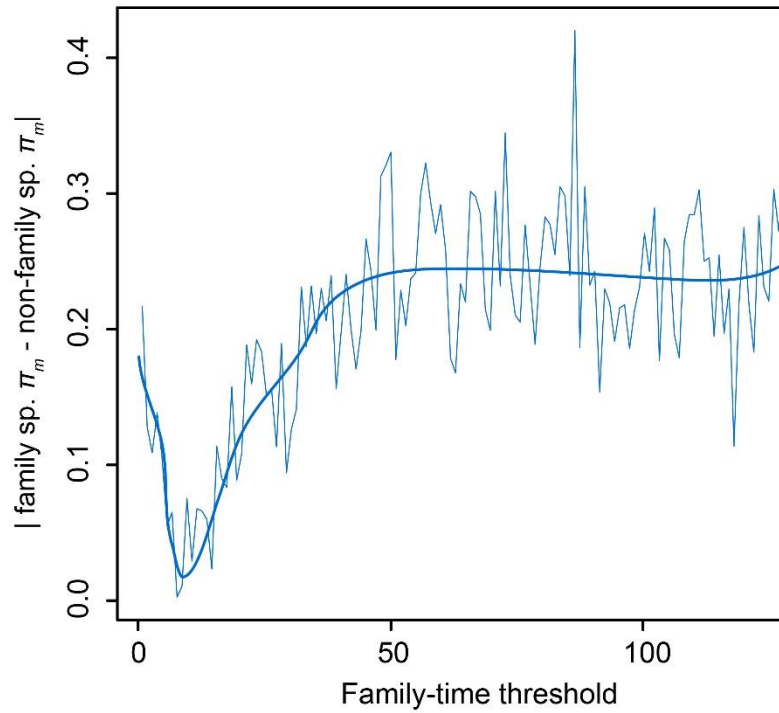
546

547 Figure S4. Changes in sample size in family (red) and non-family (green) social system group in
548 relation to changing family-time threshold used to define the two groups.

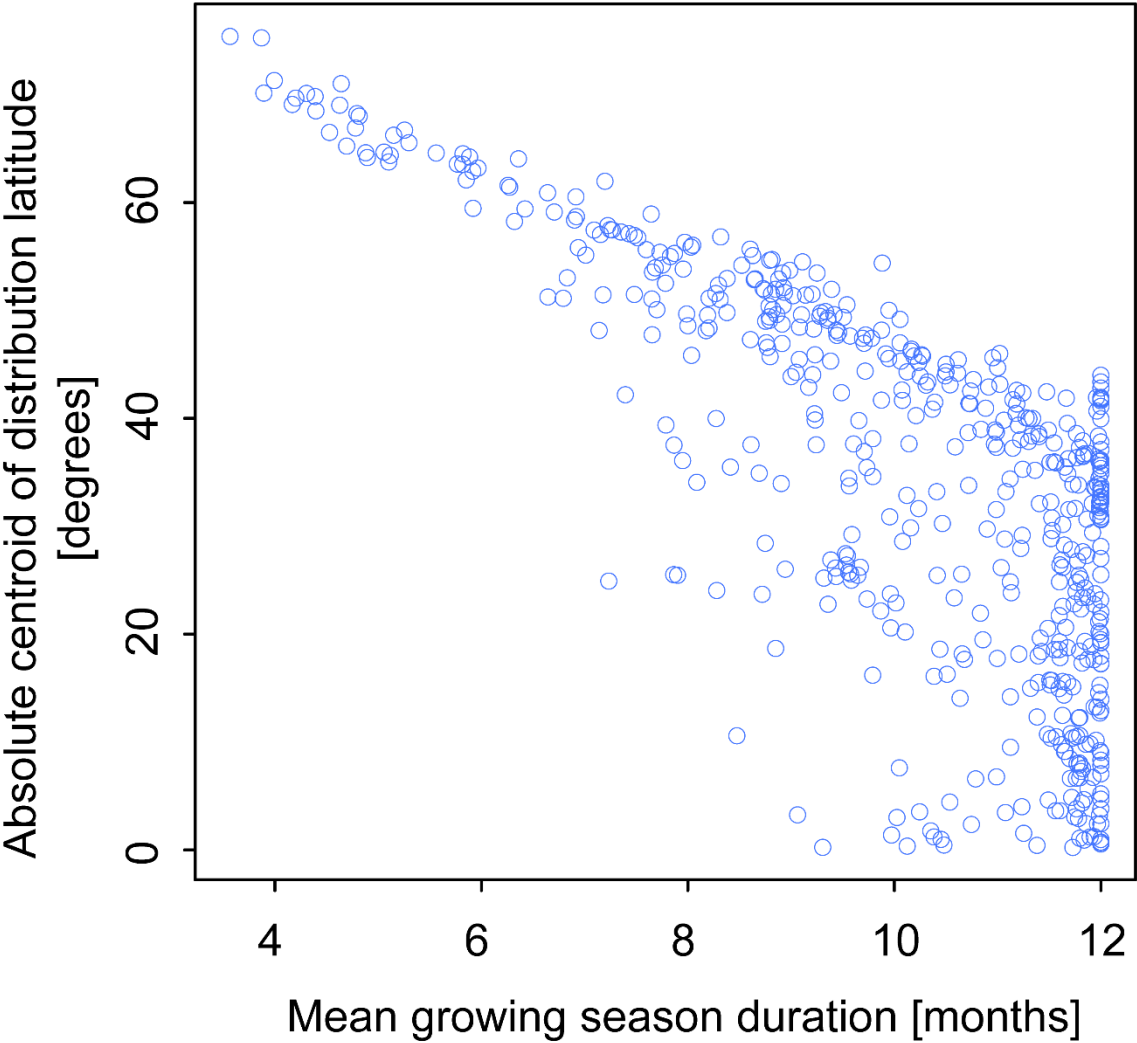


549
550
551

Figure S5. Replication of the original analysis but with resampling that ensures equal sample sizes in family-breeding and non-family-breeding group for each family-time threshold. The plot depicts relationship between the difference in productivity index between non-family and family breeding species in relation to the threshold value of family time. Thin line – original pattern, thick line – LOESS smoother fitted to the pattern to better show the overall shape. (see point 4 in validation section of Materials and methods).



560 Figure S6. Relationship between the mean growing season and the absolute latitude of the centroid of
561 geographical distribution of the included bird species.



562
563